

VARIATION OF SNAIL ASSEMBLAGES IN HAY MEADOWS: DISENTANGLING THE PREDICTIVE POWER OF ABIOTIC ENVIRONMENT AND VEGETATION

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ABSTRACT

We studied snail assemblages at 39 plots in hay meadows of the White Carpathians, Czech Republic. We recorded snails quantitatively in 1 m² quadrats, along with vegetation and several measured variables in the same plots in order to investigate the influence of selected environmental factors on meadow snail species composition and richness. The study aimed to determine the extent to which it is possible to use vegetation as a predictor of land snail composition by comparing the predictive power of three groups of variables: (i) measured variables and climatic factors, (ii) vegetation, and (iii) Ellenberg indicator values for plants estimated from plant composition.

Detrended correspondence analysis revealed that both snail and plant assemblages were strongly affected by the main environmental gradient running from calcium-poor, wet and cool upland sites to calcium-rich, dry and warm lowland sites. The main changes of vegetation and snail species composition were highly correlated ($r_s = 0.77$, $p < 0.001$). Soil calcium content and moisture were the most important factors, which explained most of the variation both in the snail and plant assemblages. The interaction of these two factors was even stronger but it was not possible to separate the influence of particular variables on snail species composition and to determine which of these variables made the greatest contribution to the observed pattern. Using the variance partitioning approach, we found that most variation in snail species data was jointly explained by all three groups of variables (i.e., measured variables and climatic factors, vegetation, and Ellenberg indicator values for plants). Even so, the net effects of both vegetation and measured variables were significant. This indicates that vegetation could describe important environmental controls of land snail distribution, even those that are difficult or even impossible to measure directly. We conclude that vegetation composition can be very useful predictor in snail community ecology studies.

Key words: gastropods, vegetation, Ellenberg indicator values, grasslands, White Carpathians.

INTRODUCTION

Hay meadows of the White Carpathian Mountains are among the most extensive and species rich grasslands in Europe (Jongepierová, 2008). In general, little work has been done on hay-meadow snail assemblages, which is probably due to low snail species richness in meadow habitats. Most snail species of temperate zone inhabit forests, which offer higher microhabitat heterogeneity (Ložek, 1956), stable micro- and mesoclimatic conditions (Martin & Sommer, 2004a) and available shelters to survive droughts and low temperatures. In forests, snails inhabit not only topsoil, but also standing woody stumps and decaying wood, cavities un-

der tree bark and leaf litter, thus they are not so closely related to soil substratum (e.g., Ložek, 1962). Except the Mediterranean region, European mollusc faunas include a limited number of species adapted to dry and open habitats (Ložek, 1964). Steppe species associated with open habitats are closely related to soil conditions and mostly require limestone formations or other calcium-rich substratum (Ložek, 1962). In contrast, Central European hay meadows are human-maintained habitats that originated after deforestation since the Neolithic (Cameron & Morgan-Huws, 1975; Chappell et al., 1971; Young & Evans, 1991). These meadows often occur on deep, originally forest soils that have lost calcium carbonate due to leaching.

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Soil calcium content and pH are in most cases considered as limiting factors that determine terrestrial gastropod distributions at various spatial scales (Burch, 1955; Horsák, 2006; Horsák & Hájek, 2003; Juříčková et al., 2008; Ložek, 1962; Valovirta, 1968; Waldén, 1981). Snails need calcium for the growth of their shells (Wärebörn, 1970) and for their successful reproduction (Wärebörn, 1979). The importance of calcium was observed also in meadow habitats where aluminum and magnesium content were also found to be important (Ondina et al., 1998, 2004). Soil texture is another important factor influencing meadow snail assemblage composition (Hermida et al., 1995; Ondina et al., 2004; Outeiro et al., 1993), along with moisture and vegetation structure (Davies & Grimes, 1999; Martin & Sommer, 2004a). All of these variables are often interrelated, and thus it is difficult to define precisely the main factor that determines land snail distribution. Especially vegetation structure and composition of meadow habitats is closely connected with land management (Cameron & Morgan-Huws, 1975; Jongepierová, 2008). The impact of different management practices and vegetation succession on snail assemblages was observed in several studies (Baur et al., 2006; Boschi & Baur, 2008; Cremene et al., 2005; Labaune & Magnin, 2002; Ruesink, 1995). In general, vegetation structure was found to be more important explanatory factor than floristic composition because microclimate conditions are more related to vegetation structure than to plant species composition (Labaune & Magnin, 2001). Other studies showed that vegetation composition was more important for explaining variation in snail species of spring fens than water chemistry (Horsák & Hájek, 2003; Horsák et al., 2011). It was also shown that plant indicator values (Ellenberg et al., 1992) were a useful tool for land mollusc autecology assessment (Horsák et al., 2007b).

Thus, it is not surprising that the gross distribution of both snails and plants relate to the same environmental gradients. The questions remain as to possible differences at small scales, and the extent to which explanatory variables based on plant species composition can act as surrogates for others that are harder or more expensive to obtain. Therefore, we recorded both snails and plants inhabiting the same plot in the same time. Further, for the explanation of variation in snail assemblages we not only used several directly measured factors but also variables obtained from vegetation composition.

We established three main aims of this study: (i) to investigate the influence of selected environmental factors on snail species composition and richness in hay meadows, (ii) to determine to what extent it is possible to use vegetation as a predictor of land snail composition by comparing the predictive power of three groups of variables: measured variables and climatic factors, vegetation, and Ellenberg indicator values for plants, and (iii) to compare effects of the studied factors between snail and plant assemblages.

MATERIAL AND METHODS

A total of 39 plots distributed in 27 localities were studied in dry grasslands and mesic meadows in the White Carpathians Mountains, southeastern Czech Republic (Fig. 1) in 2005–2008. The extent of the study area is 715 km². Geologically it belongs to the outer part of the Western Carpathians, mostly to the Magura Flysch. This is bedrock formed by Cretaceous and Palaeogene sea sediments consisting of alternating sandstone and claystone layers of variable thickness (Jongepierová, 2008). These sediments often contain a considerable amount of calcium carbonate, but most of the studied meadows have developed on originally forest soils and have a secondarily decalcified topsoil layer. Exceptions are small patches with shallow soils around the outcrops of calcareous bedrock. There are also climatic and historical differences within the study area. Altitude and precipitation increase and temperature decreases towards the northeast. The studied localities are at altitudes 296–667 m and have average annual precipitation amounts of 555–907 mm and average annual temperatures of 6.8–8.5°C. Geographical influences and altitude are closely connected with historical development of the area. Meadows at higher altitudes, especially in the northeastern part of the study area, have originated later than meadows in lowlands in the southwest due to the different timing of human settlement (Jongepierová, 2008). The vegetation of these meadows has been classified into three phytosociological alliances (Jongepierová, 2008): (i) the subcontinental broad-leaved dry grasslands of *Cirsio-Brachypodium pinnati* Hadač et Klika ex Klika, 1951, (ii) subatlantic broad-leaved dry grasslands of *Bromion erecti* Koch, 1926, and (iii) mesic meadows of *Arrhenatherion elatioris* Luquet, 1926.

All studied meadows are managed by mowing twice a year, only exceptionally once a year

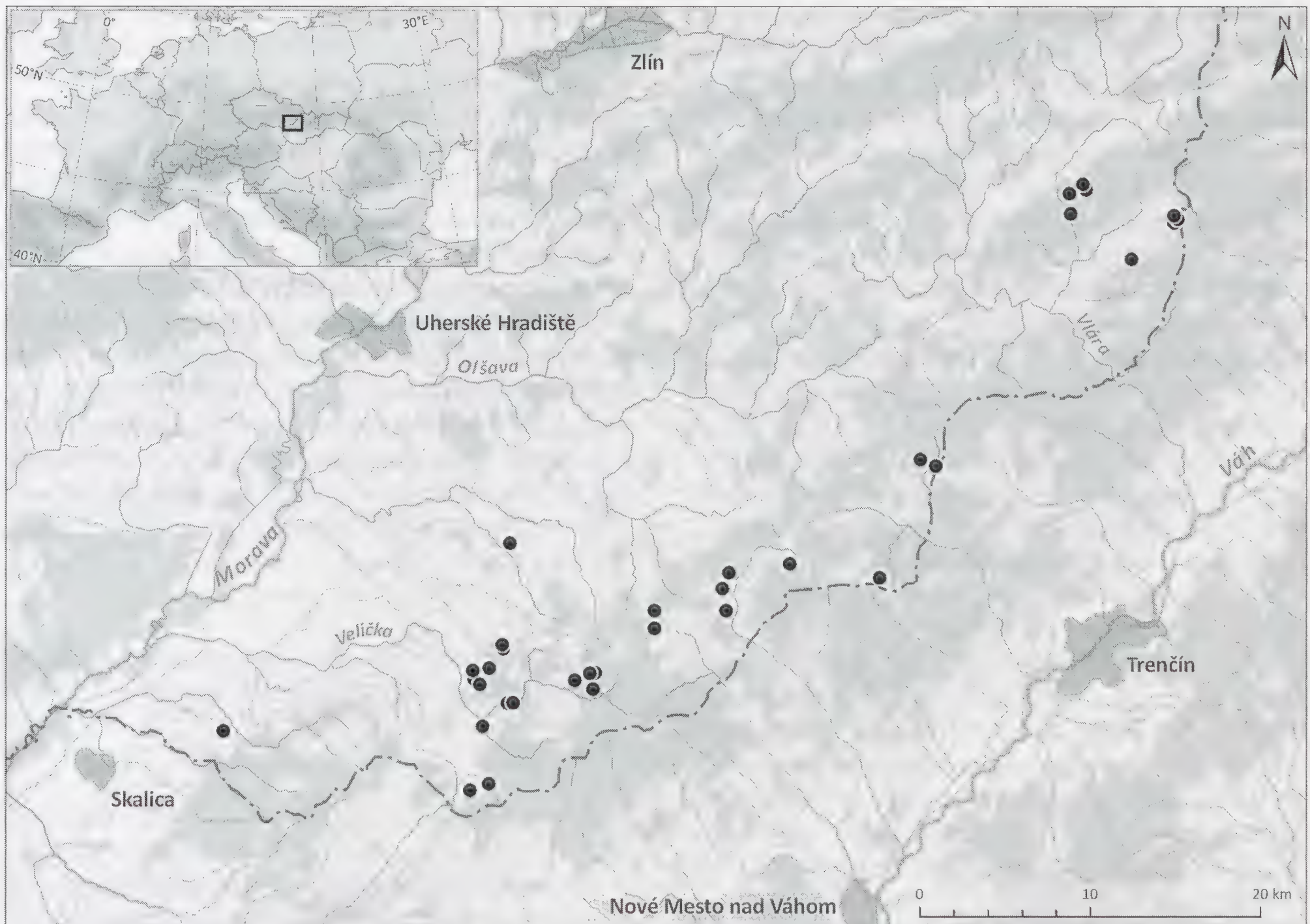


FIG. 1. Map of the studied area with 39 study sites marked by points.

in the case of driest meadows with sparse vegetation. All plots of 1 m² were sampled in spring, mostly at separated meadow sites in order to avoid pseudoreplications. In each plot, cover of all vascular plant species was recorded on the nine-grade Braun-Blanquet scale (Westhoff & van der Maarel, 1978). Then, in each plot, the upper soil layer up to the depth of 5 cm was taken from four randomly chosen 25 x 25 cm quadrats for quantitative sampling of snail assemblages. After snail sampling, topsoil samples were collected from each plot for laboratory measurements of soil calcium content and pH. A 2:5 soil-distilled water solution was prepared from each sample and measured after 20 h by a pH-meter. A 1:10 Mehlich III solution was filtered after ten minutes of shaking, and soil calcium content was measured by an atomic absorbing spectrophotometer in an accredited laboratory. The snail samples were dried and then extracted using standard procedures and separated by hand-sorting under a binocular microscope (Kerney et al., 1983; Ložek, 1956). Live snails and empty shells were counted separately. Counts from four quadrats

of each 1 m² plot were merged together. Soil moisture was measured in the field in October 2008 by one-shot measurement at each plot during three days of stable dry weather without precipitation. We used Theta Probe ML2x hygrometer, which measures moisture of the topsoil layer up to the depth of 10 cm.

In total, we used 22 explanatory variables which were divided into three groups: (i) Group I, which includes measured soil variables (soil pH, soil calcium content and soil moisture), further basic climatic factors (mean annual precipitation and mean annual temperatures) obtained from digital maps of climatic factors (Tolasz, 2007) by overlying them in the geographic information systems (ESRI, 2003), topographic indices of solar radiation and heat load (radiation, heat) calculated from the slope, aspect and geographic coordinates (McCune & Keon, 2002), altitude, latitude and longitude; (ii) Group II, consisting of variables obtained based on Ellenberg's indicator system (EIVs) used in vegetation science (e.g., Ertsen et al., 1998; Ewald, 2003; Hill & Carey, 1997; Schaffers & Sýkora, 2000; Wamelink et al., 2002).

EIVs are empiric values assigned to each of 2726 Central European vascular plant species to reflect their ecological behaviour. EIVs express, on an ordinal scale, the relationship of plant species to chosen ecological gradients (E-light, E-temperature, E-continentality, E-moisture, E-reaction, and E-nutrients). This scale is 12-point for moisture and a 9-point for the other variables (Ellenberg et al., 1992). The value for each plot was calculated as an average of all values of each plant species recorded in the plot; (iii) Group III, vegetation; variables expressing vegetation structure (the cover of herbs and mosses) and plant species composition expressed as the ordination site scores on the first four DCA (Detrended correspondence analysis) axes (V1DCA–V4DCA; see below).

The relationships among explanatory variables were summarized using principal component analysis (PCA) on a correlation matrix calculated using STATISTICA 7 (Hill & Lewicki, 2007). The snail data were adjusted before statistical analyses. All slugs (two species) were omitted because our sampling method did not allow accurate assessment of their occurrence and abundance (Oggier et al., 1998). For multivariate analyses, we used numbers of live individuals, because abundance of empty shells is strongly influenced by levels of soil calcium (Cernohorsky et al., 2010; Claassen, 1998) and can be also linked with decay time of shells of particular species (Ménez, 2002; Pearce, 2008). We also used in the analyses species with no live individual recorded in the particular site, but only those where at least one freshly dead shell (i.e., with an intact periostracum) was recorded. Therefore, we added 1 to the number of live individuals of each recorded species; the abundance of species recorded only as fresh empty shell(s) was equal to 1. This allowed to capture also low-abundant living species, which were very probably present at studied plots, but not recorded as live by sampling. Abundances were log-transformed as $Y = \log(n + 1)$ to undo the influence of dominant species. Rare species were down-weighted as recommended for DCA (Lepš & Šmilauer, 2003). For multivariate analyses of vegetation, we used untransformed estimates of cover.

The species-by-plot matrices for snail and plant samples were separately subjected to DCA. The ordination site scores obtained were correlated with each other and with explanatory variables using the Spearman correlation coefficient. Canonical correspondence analysis (CCA) and the variation partitioning approach (Borcard et al., 1992) were used to segregate variation of snail

data among three groups of variables (measured variables, EIVs, vegetation). In the first step, we used CCA and a forward selection method to isolate three best predictors out of each group because explained variation is also influenced by the number of explanatory variables (Peres-Neto et al., 2006). These variables explained most variation within snail assemblages. In the next step, we used partial CCAs and the variation partitioning approach to segregate variation among these nine variables. Significance of the canonical axes was testing by Monte Carlo test with 1,999 permutations. The multivariate analyses were done using the CANOCO 5 package (ter Braak & Šmilauer, 2002). Spearman correlation coefficient was calculated in STATISTICA 7 (Hill & Lewicki, 2007).

TABLE 1. Coordinates of 22 explanatory variables on the first two axes of PCA on correlation matrix of 39 plots. Significance is given as: n.s. - not significant; * - $p < 0.05$; ** - $p < 0.01$.

Explanatory variables	1st PCA axis	2nd PCA axis
Eigenvalue	8.316	3.621
Percentage variance explained	37.8	16.46
Latitude	n.s.	0.81**
Longitude	-0.51*	0.79**
Soil pH	0.70**	n.s.
Soil calcium content	0.78**	n.s.
Soil moisture	-0.46*	-0.47*
Altitude	-0.77**	0.33*
Mean annual temperature	0.75**	-0.51*
Mean annual precipitation	-0.78**	0.34*
Radiation	0.43*	0.52*
Heat	0.42*	0.49*
E-light	0.62**	0.45*
E-temperature	0.70**	n.s.
E-continentality	0.70**	n.s.
E-moisture	-0.77**	n.s.
E-reaction	0.84**	n.s.
E-nutrients	-0.63**	-0.52*
V1DCA	-0.91**	n.s.
V2DCA	n.s.	n.s.
V3DCA	n.s.	n.s.
V4DCA	n.s.	n.s.
Moss cover	-0.33*	n.s.
Herb cover	-0.64**	n.s.

RESULTS

Table 1 shows the relationships of the explanatory variables to the first and second PCA axes; however, most of the measured explanatory variables were closely interrelated. PCA detected a strong environmental gradient associated with the first axis, running from calcium poor, wet, cold and upland sites to the calcium rich, dry, warm and lowland sites with lower precipitation (Table 1). The second PCA axis reflected the geographical gradient from the northeastern to southwestern part of the White Carpathian Mountains. The third and higher axes explained a very small part of the total variation and their correlations with individual variables were not significant.

The studied snail assemblages were rather poor in species. In total, we found 29 snail species and collected 5,285 live individuals and 13,662 empty shells (Table 2). On average 5 (min. 4, max. 10) live snail species and 117 (min. 13, max. 621) live individuals per plot were collected. Numbers of species as well as numbers of individuals were strongly correlated with soil calcium content, pH and E-reaction (Table 3). We observed a higher predictive power of the interaction between measures of calcium and site moisture.

Snail species composition and its relation to explanatory variables were studied using DCA. We obtained only one strong gradient of snail species composition, which was mainly associated with E-moisture ($r_s = 0.75$; $p < 0.001$),

TABLE 2. List of all analysed species, frequency of live and all individuals at study 39 sites, number of all live individuals, and number of all empty shells.

Species	Freq. of live individuals	Freq. of all individuals	No. of live individuals	No. of empty shells
<i>Punctum pygmaeum</i> (Draparnaud, 1801)	38	39	1048	2715
<i>Vertigo pygmaea</i> (Draparnaud, 1801)	31	35	962	2607
<i>Cochlicopa lubricella</i> (Rossmässler, 1838)	27	31	398	762
<i>Vallonia pulchella</i> (Müller, 1774)	24	29	562	1273
<i>Vitrina pellucida</i> (Müller, 1774)	21	24	509	513
<i>Perpolita hammonis</i> (Ström, 1765)	21	27	166	349
<i>Truncatellina cylindrica</i> (Férussac, 1807)	19	21	1177	2903
<i>Euomphalia strigella</i> (Draparnaud, 1801)	16	29	73	110
<i>Granaria frumentum</i> (Draparnaud, 1801)	7	8	22	1105
<i>Acanthinula aculeata</i> (Müller, 1774)	7	11	48	210
<i>Cochlicopa lubrica</i> (Müller, 1774)	6	9	39	65
<i>Vallonia costata</i> (Müller, 1774)	5	9	167	255
<i>Aegopinella minor</i> (Stabile, 1864)	5	14	30	419
<i>Vitrea contracta</i> (Westerlund, 1871)	2	8	6	84
<i>Euconulus fulvus</i> (Müller, 1774)	1	4	1	6
<i>Cepaea vindobonensis</i> (Férussac, 1821)	1	4	5	35
<i>Cecilioides acicula</i> (Müller, 1774)	1	2	19	170
<i>Oxychilus inopinatus</i> (Uličný, 1887)	1	1	5	4
<i>Carychium tridentatum</i> (Risso, 1826)	1	2	1	25
<i>Vertigo angustior</i> Jeffreys, 1830	1	3	43	35
<i>Petasina unidentata</i> (Draparnaud, 1805)	1	1	2	1
<i>Pupilla muscorum</i> (Linnaeus, 1758)	0	4	0	7
<i>Carychium minimum</i> Müller, 1774	0	2	0	2
<i>Alinda biplicata</i> (Montagu, 1803)	0	2	0	2
<i>Aegopinella pura</i> (Alder, 1830)	0	1	0	1
<i>Vertigo pusilla</i> Müller, 1774	0	1	0	3
<i>Vitrea diaphana</i> (Studer, 1820)	0	1	0	1

TABLE 3. Spearman correlations among species data and explanatory variables (including their interactions - x). Significance is given as: n.s. - not significant; * - $p < 0.05$; ** - $p < 0.01$.

Explanatory variables	No. of live individuals	No. of live species	No. of all individuals	No. of all species
Soil pH	n.s.	n.s.	0.51*	0.39*
Soil calcium content	0.45*	n.s.	0.66**	0.46*
Soil moisture	n.s.	n.s.	n.s.	n.s.
Altitude	n.s.	n.s.	-0.40*	-0.43*
Mean annual precipitation	n.s.	n.s.	n.s.	n.s.
Mean annual temperature	n.s.	n.s.	0.37*	0.34*
Radiation	n.s.	n.s.	n.s.	n.s.
Heat	n.s.	n.s.	0.33*	n.s.
E-light	n.s.	n.s.	0.36*	n.s.
E-temperature	n.s.	n.s.	0.33*	n.s.
E-continentality	n.s.	n.s.	n.s.	n.s.
E-moisture	n.s.	n.s.	n.s.	n.s.
E-reaction	n.s.	n.s.	0.48*	0.41*
E-nutrients	n.s.	0.41*	n.s.	n.s.
Soil calcium content x moisture	0.47*	n.s.	0.67**	0.48*
Soil calcium content x E-moisture	0.47*	0.32*	0.68**	0.49*
E-reaction x E-moisture	n.s.	0.52**	n.s.	0.34*

E-nutrients ($r_s = 0.62$; $p < 0.001$), altitude ($r_s = 0.62$; $p < 0.001$), annual precipitation ($r_s = 0.61$; $p < 0.001$), and E-reaction ($r_s = 0.61$; $p < 0.001$)

(Table 4, Fig. 2). This change of snail species composition was also strongly associated with the main change of plant species composition

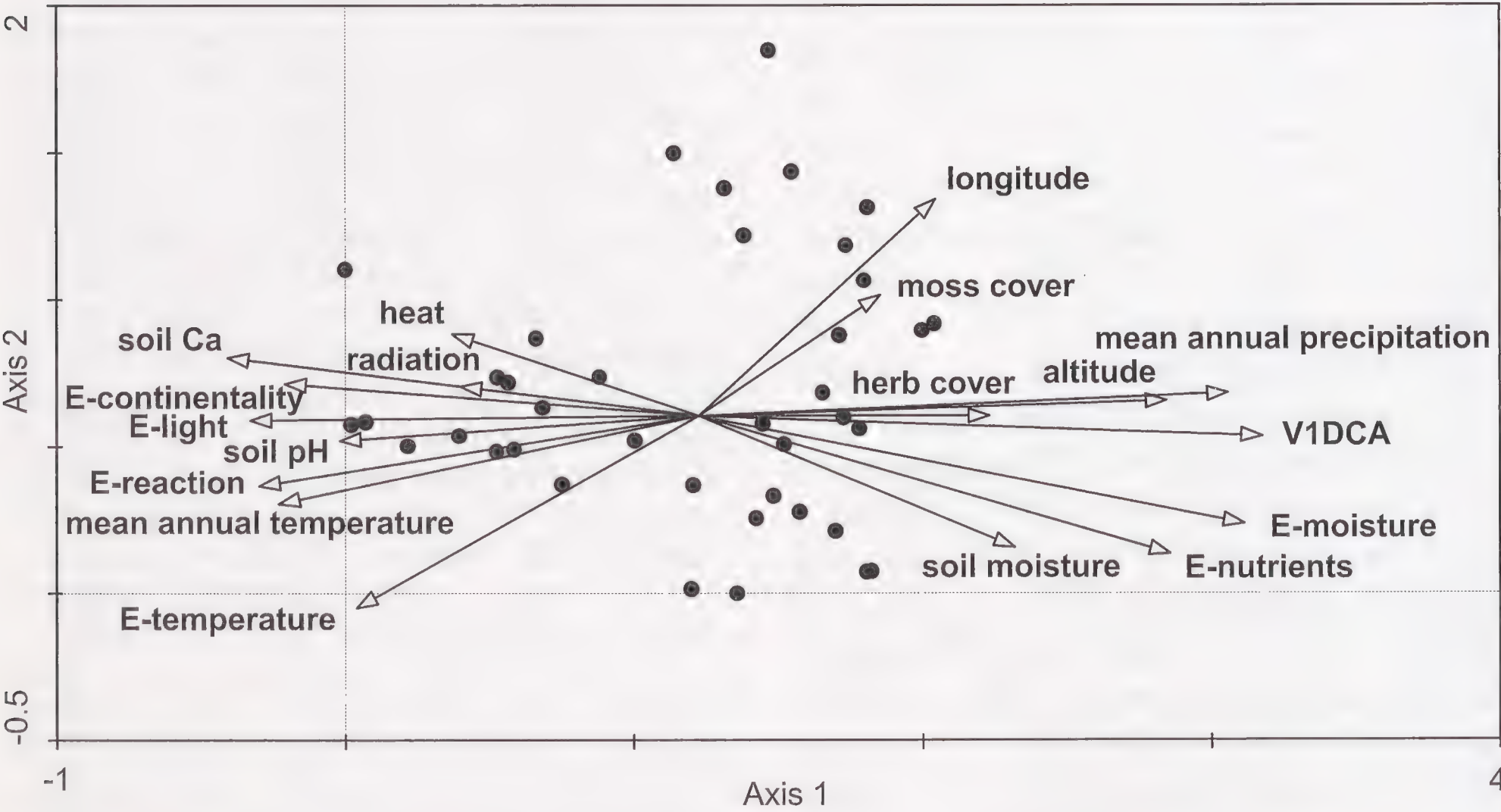


FIG. 2. Detrended correspondence analysis (DCA) of snail assemblages: ordination plot of sites on the first two DCA axes. The first two DCA axes explained 34.5% of total variation in snail data (first axis 24.7%). Only variables significantly related to species composition ($p < 0.05$) are shown.

TABLE 4. Correlations between the first two DCA axes and all explanatory variables. Significance is given as: n.s. - not significant; * - $p < 0.05$; ** - $p < 0.01$.

Explanatory variables	1st DCA	2nd DCA
Latitude	n.s.	n.s.
Longitude	0.47*	n.s.
Soil pH	-0.45*	n.s.
Soil calcium content	-0.51**	n.s.
Soil moisture	0.40*	n.s.
Altitude	0.62**	n.s.
Mean annual temperature	-0.55**	n.s.
Mean annual precipitation	0.60**	n.s.
Radiation	-0.38*	n.s.
Heat	-0.35*	n.s.
E-light	-0.52**	n.s.
E-temperature	-0.49*	-0.39*
E-continentality	-0.59**	n.s.
E-moisture	0.75**	n.s.
E-reaction	-0.61**	n.s.
E-nutrients	0.62**	n.s.
V1DCA	0.77**	n.s.
V2DCA	n.s.	n.s.
V3DCA	n.s.	n.s.
V4DCA	n.s.	n.s.
Moss cover	0.38*	0.33*
Herb cover	0.39*	n.s.

(V1DCA; $r_s = 0.77$; $p < 0.001$). Site scores on the second DCA axis of the snail data were only weakly correlated with E-temperature

and moss cover (Table 4). Calcium-poor but wet sites, lying often at high altitudes with high precipitation, were placed on the right side of the diagram (Fig. 2). At these sites we found only few common species in a low abundance, in particular *Perpolita hammonis*, *Vitrina pellucida*, *Vallonia pulchella* and *Cochlicopa lubrica* (Fig. 3). The calcium-rich but dry sites with open vegetation were on the left side of the diagram. These sites were inhabited by species that preferred sites with warm conditions. They were also species-poor, but they hosted such typical steppe species as *Granaria frumentum* and *Truncatellina cylindrica* (Fig. 3). These differences are linked with different responses of several species to the studied variables (Table 5). Abundance of *Granaria frumentum* and *Truncatellina cylindrica* were positively correlated with calcium content and negatively with moisture. In contrast, abundances of *Perpolita hammonis* and *Vitrina pellucida* were positively correlated with moisture and indifferent to calcium content.

Variation among snail assemblages was significantly associated with variables in all three analysed groups. Table 6 shows the nine variables which explained most variation in snail data and were used in partial CCA analyses. The resulting diagram (Fig. 4) shows that most of the variation in snail data was shared by all groups of variables (11%). Each group had its own contribution; however, the independent variation explained by EIVs was not significant. An exclusive and independent proportion of snail data variation was explained by the main change of plant species composition (V1DCA). A significant and exclusive contribution of soil calcium content within measured variables was also of high importance.

TABLE 5. Spearman correlations between species abundances and explanatory variables. Significance is given as: n.s. - not significant; * - $p < 0.05$; ** - $p < 0.01$. Abbreviation: GraFru, *Granaria frumentum*; PerHam, *Perpolita hammonis*; TruCyl, *Truncatellina cylindrica*; VitPel, *Vitrina pellucida*.

Explanatory variables	GraFru	TruCyl	PerHam	VitPel
Soil calcium content	0.61**	0.71**	n.s.	n.s.
Soil pH	0.55**	0.55**	n.s.	n.s.
E-reaction	0.58**	0.69**	n.s.	n.s.
Soil moisture	n.s.	-0.54**	n.s.	0.32*
E-moisture	-0.50*	-0.58**	0.51**	0.50*

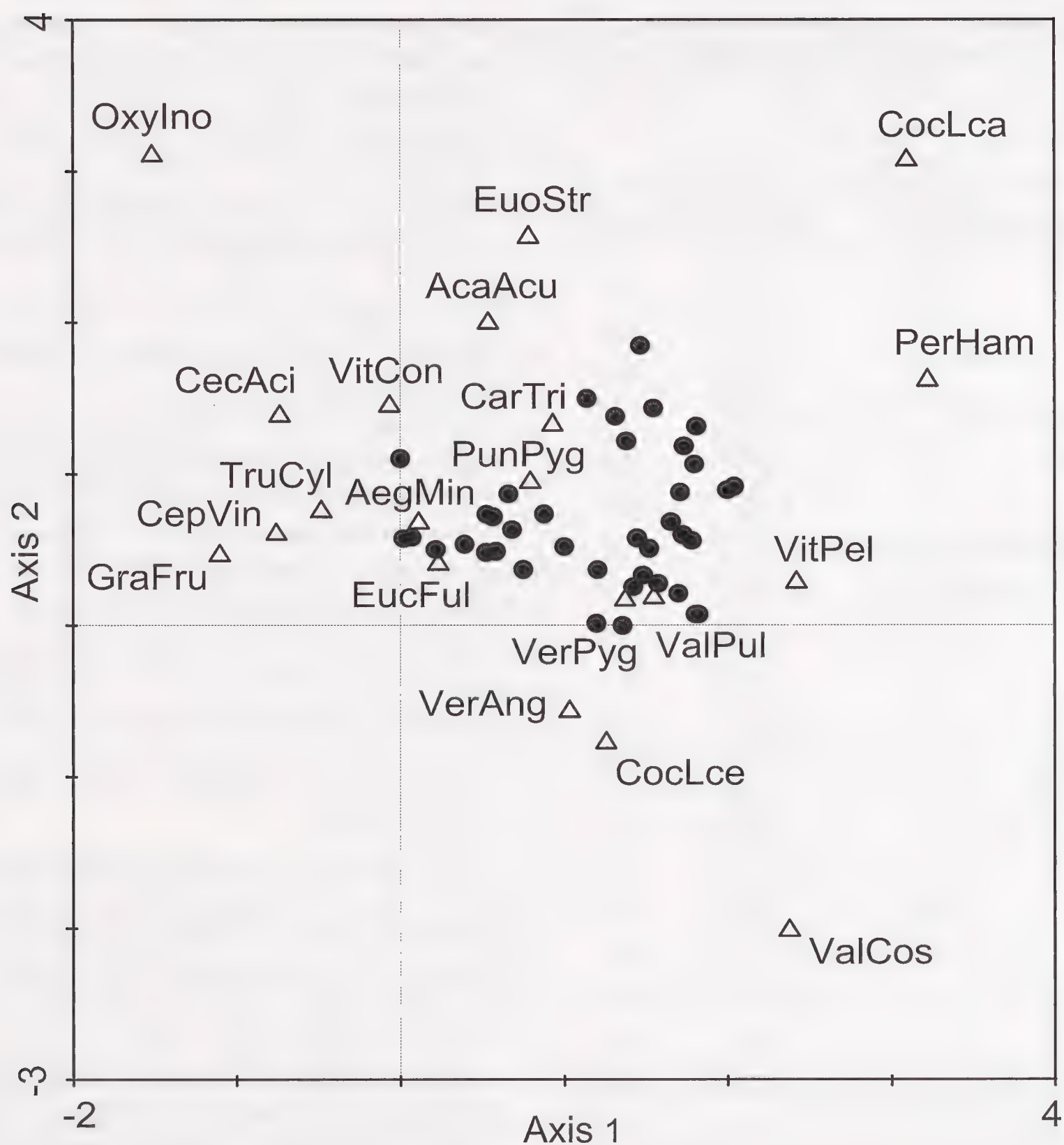


FIG. 3. Detrended correspondence analysis (DCA) of snail assemblages: ordination plot of species on the first two DCA axes. Abbreviation: AcaAcu, *Acanthinula aculeata*; AegMin, *Aegopinella minor*; CecAci, *Cecilioides acicula*; CepVin, *Cepaea vindobonensis*; CocLca, *Cochlicopa lubrica*; CocLce, *Cochlicopa lubricella*; EucFul, *Euconulus fulvus*; EuoStr, *Euomphalia strigella*; GraFru, *Granaria frumentum*; OxyIno, *Oxychilus inopinatus*; PerHam, *Perpolita hammonis*; PunPyg, *Punctum pygmaeum*; TruCyl, *Truncatellina cylindrica*; ValCos, *Vallonia costata*; ValPul, *Vallonia pulchella*; VerAng, *Vertigo angustior*; VerPyg, *Vertigo pygmaea*; VitCon, *Vitrea contracta*; VitDia, *Vitrea diaphana*; VitPel, *Vitrina pellucida*.

DISCUSSION

In this study, the relative importance of different variables in structuring the snail fauna was hard to determine because the relevant variables were highly intercorrelated (Table 1). The same conclusion has been reached in most studies on ecology of land snails (e.g., Labaune & Magnin, 2001). High positive correlations of variables reflecting similar conditions (calcium content, E-reaction, pH) were not surprising, but negative correlation of soil calcium content and moisture was a more interesting finding.

Most of the studied meadows were both calcium poor and wet and the calcium poorest and wettest sites lay in high-altitude areas with high precipitation. All those sites occurred on deep, originally forest soils and it is likely that they lost calcium carbonate due to cation leaching (Otýpková et al., 2011).

Snail species composition was strongly affected by variables expressing site moisture, calcium content, and altitude (Table 4). This finding is consistent with the results of many previous studies (Davies & Grimes, 1999; Horsák 2006; Martin & Sommer, 2004a, b)

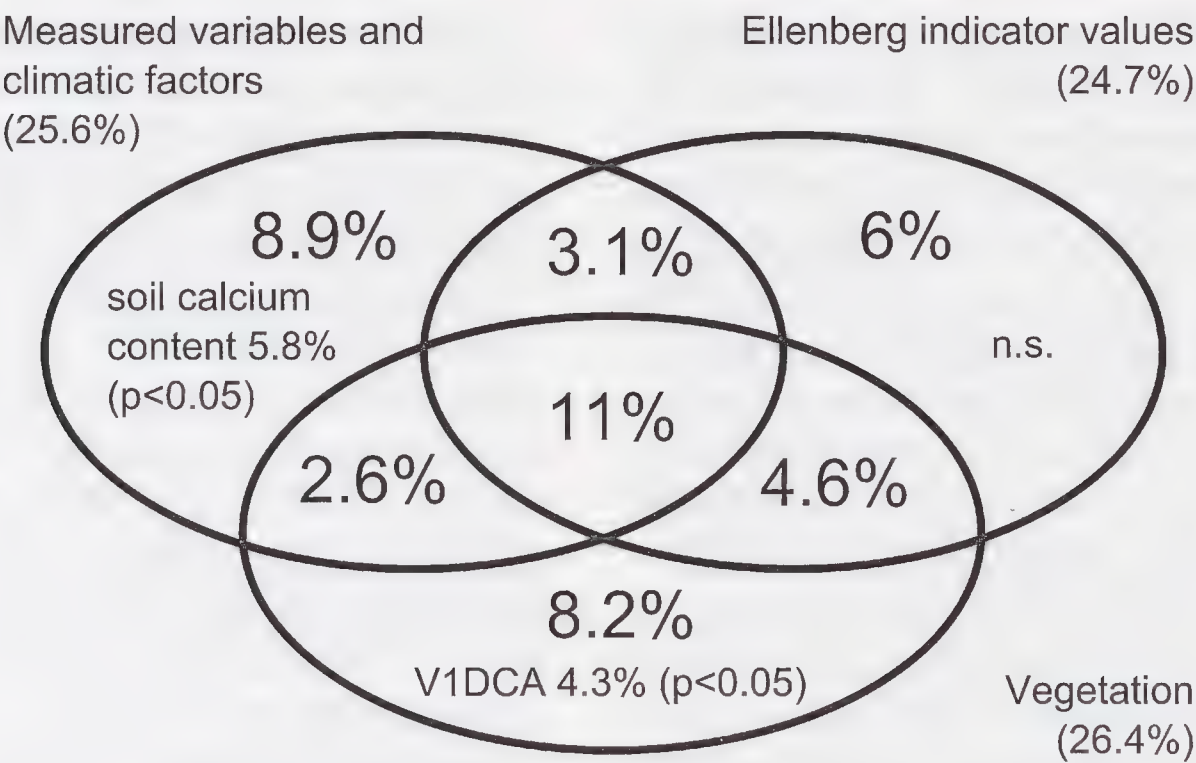


FIG. 4. Venn diagram of variation partitioning among three groups of variables (each consisting of three variables; see Table 6).

and confirms strong dependence of snails on site conditions. However, there are at least two reasons why it is impossible to disentangle the effects of three above mentioned factors. Firstly, these factors all reflect a single ecological gradient and all these factors are known to control snail species composition. The wetter sites were also calcium poor, and thus they supported only few, low abundant common species. Dry and calcium rich sites were also species poor; nevertheless, they hosted exclusively steppe species though they were too dry for the occurrence of other more common generalist species. We observed high predictive power of an interaction between soil calcium content and soil moisture for both snail abundances and species composition (Tables 3, 5), which was strengthened by various responses of individual species to these factors (Hermida et al., 1995; Ondina et al., 1998, 2004; Outeiro et al., 1993). In this study, low soil calcium content was the limiting factor for *Granaria frumentum* and *Truncatellina cylindrica*, low soil moisture was limiting factor for *Perpolita hammonis* and *Vitrina pellucida*.

Studies on spring fen communities, where the soil moisture is permanently high, suggested that *T. cylindrica* inhabits wet fens if calcium carbonate content is very high (Horsák, 2006; Horsák & Hájek, 2003). In contrast, *G. frumentum* occurred only in dry meadows with high soil calcium content. *Perpolita hammonis* and *V. pellucida* occurred along the whole mineral poor-rich gradient of the fens, but they had low abundance in the driest meadows or were totally absent there.

The main change in snail assemblage composition was explained not only by directly measured variables and climatic factors but also by their estimates on the basis of Ellenberg indicator values and by changes in plant species composition. It is obvious that snails and plants living at the same plot in the same time are affected by the same environmental conditions; thus, species composition of their assemblages is probably determined by similar environmental factors. This is in accordance with our results. We observed that the main change of snail species composition and plant species composition (both expressed as site

TABLE 6. Variables selected in forward selection (CCA, Monte Carlo test, $p < 0.01$) as the most important for explaining variation in snail species data and percentage of independent variation in snail data explained by each variable.

Measured variables and climatic factors		Ellenberg indicator values		Vegetation	
Mean annual precipitation	13.8%	E-moisture	13.4%	V1DCA	15.6%
Soil calcium content	6.8%	E-reaction	7.0%	V4DCA	5.6%
Soil moisture	5.0%	E-temperature	4.3%	V3DCA	4.8%

scores on the 1st DCA axis) were highly correlated ($r_s = 0.77$, $p < 0.001$). Consequently, we used the variance partitioning approach to analyse the extent to which it is possible to use vegetation as a predictor of land snail composition. We found that most variation in snail species data was shared by all three groups of variables: directly measured variables, changes in plant species composition, and Ellenberg indicator values (Fig. 4). However, pure effects of both vegetation and measured variables were significant. This indicates that vegetation can effectively describe those factors that were not recorded or probably that are difficult or even impossible to directly measure. These factors include among others historical development, site management and biogeographical patterns. Nevertheless, these hidden factors can influence both vegetation and snail assemblages in the same ways and thus shape their species composition. A high level of concordance in species composition of plants and snails was also found in the Western Carpathian spring fens, where vegetation was able to predict the composition of mollusc assemblages even better than measured water chemistry parameters (Horsák & Hájek, 2003). Historical development of these fens influenced distribution of relict plant and snail species, which are significantly related to old sites with Late Glacial continuity (Hájek et al., 2011). This is the main reason for a sharp geographical gradient within a rather small area, independently of any climatic or other environmental variation (Horsák et al., 2007a). Magnin et al. (1995) found similar patterns, related to the landscape dynamic effect on snail and plant assemblages.

In our study, the significant and exclusive contribution of soil calcium content shows that it is impossible to estimate completely the effect of calcium content based on vegetation and Ellenberg IVs. This raises an interesting question that plants and snails could uptake calcium from different soil layers. In most of the studied meadows, the surface layer is decalcified and the content of calcium increases with soil depth (Dvořáková, unpubl. data; Jongepierová, 2008). In contrast, Ellenberg soil reaction values were better correlated with the first DCA axis of snail species composition than soil pH and calcium content. The same pattern was observed by Horsák et al. (2007b), who identified Ellenberg soil reaction values as the best predictor of fen mollusc species composition. However, a pure effect of EIVs for soil reaction

in the present study was not significant, probably because of their similarity with the group of variables reflecting plant species composition gradients (expressed as three significant DCA axes; Fig. 4, Vegetation, 4.6%). Corresponding with Horsák et al. (2007b), Ellenberg indicator values for some environmental variables has even higher predictive power than directly measured values. A high level of intercorrelation between variables obtained from plant species composition and directly measured factors confirmed that data on vegetation can act as a proxy for the general environmental regime and its effect on snail faunas.

However, it is not surprising that in general it is difficult to disentangle the influence of vegetation structure (i.e., mean height, proportion of bare ground, proportion of vascular plant and bryophyte cover) and species composition because vegetation structure strongly depends on particular plant species, and plant species occurrences are controlled by vegetation structure due to the competitive exclusion. In our study, we used the cover of herbs and mosses as variables describing vegetation structure, but we suggest that better information about vegetation structure is contained mostly in species composition. Several studies showed that also occurrence and abundance of snail species dependent on vegetation structure mainly because of food source, microclimate and presence of available shelters (Boycott, 1934; Cameron et al., 1980; Labaune & Magnin, 2001). However, these studies pointed out that the possible relationships between snail and plant assemblages are more dependent on microclimate conditions controlled by vegetation structure than on plant species composition itself. On the contrary, our results support different hypothesis that even vegetation composition can be very useful predictor of variation in snail assemblages.

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